A battle of wits? Problem-solving abilities in invasive Eastern grey squirrels and native Eurasian red squirrels.

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ABSTRACT

Behavioural flexibility has been argued to be an evolutionarily favourable trait that helps invasive species to establish themselves in non-native environments. But few studies have compared the level of flexibility (whether considered as an outcome or as a process) in mammalian invaders and related native species. Here, we tested whether flexibility differs between groups of free-ranging invasive Eastern grey squirrels (*Sciurus carolinensis*) and native Eurasian red squirrels (*S. vulgaris*) in the UK, using an easy and a difficult food–extraction task. All individuals of both species showed flexibility, at the outcome level, in solving the easy task and solution time was comparable between species across a series of successes. A higher proportion of grey squirrels than red squirrels solved the difficult task. However, for those squirrels that did solve the task, solving efficiency was comparable between species on their first success, and a few red squirrels outperformed the grey squirrels in subsequent successes. Between species analysis showed that instantaneous flexibility, flexibility at the process level that was measured as the rate of switching between tactics after a failed attempt, was higher in red squirrels than in grey squirrels. Within species analysis also revealed that red squirrel problem solvers showed higher flexibility at the process level, than their non-solver counterparts. Non-solvers also failed to make 'productive' switches (switching from ineffective tactics to effective tactics). Together, the results suggest that problem-solving ability overlaps in the two species, but is less variable, and on average higher, in grey squirrels than in red squirrels. The superior behavioural flexibility of the grey squirrels, shown here by success at problem solving, may have facilitated their invasion success, but it may also have resulted from selective pressures during the invasion process.

Keywords: behavioural flexibility, invasive and native species, problem solving, squirrels

INTRODUCTION

Behavioural flexibility has been argued to be an evolutionarily favourable trait for invasive species, as flexibility helps them adapt to non-native environments (e.g. Jarić, Jaćimović, Cvijanović, Knežević-Jarić, & Lenhardt, 2014; Webb, Letnic, Jessop, & Dempster, 2014; Lefebvre, Reader, & Sol, 2013; Sol, Timmermans, & Lefebvre, 2002; Sol & Lefebvre, 2000). Flexibility has been measured in a number of ways (see review by Audet & Lefebvre, 2017), and it has been conceptualised at different levels. On the one hand, it has been conceived as a process (hereafter, 'the process level') through which animals are able to vary their behaviours (e.g. Benson-Amram & Holekamp, 2012; Chow, Lea, & Leaver, 2016; Chow, Lea, Hempel, & Robert, 2017; Griffin, Diquelou, & Perea, 2014). For example, Lefebvre and colleagues have measured flexibility from the incidence of novel foraging techniques per taxon (Lefebvre et al., 2013; Sol et al., 2002; Sol & Lefebvre, 2000). On the other hand, flexibility has been conceived as an outcome of actions observed when animals show variations in responding to challenges (hereafter, 'the outcome level'). For example, flexibility could be measured as the outcome of success or failure in solving artificial problem-solving tasks (review by Griffin & Guez, 2014) in which animals are required to overcome obstacles to obtain food rewards, either by applying previously learned tactics to solve a novel problem, or by developing novel tactics to solve old problems (Kummer & Goodall, 1985; Reader & Laland, 2003). In practice, the process can be also inferred from its behavioural outcome, for example, enhanced flexibility is indicated by success in solving artificial problem tasks.

Both these approaches have been used to suggest a relationship between flexibility and success as an invasive species. Sol et al. (2002) and Sol and Lefebvre (2000) have shown that, across taxa, the incidence of novel foraging techniques reported is correlated with the

establishment of invasive bird species in new environments, while Griffin and Diquelou (2015) have used artificial problem–solving tasks to examine the level of flexibility in two successfully invasive bird species, Indian mynas (*Acridotheres tristis*) and noisy mynas (*Manorina melanocephala*). In the present paper, we take a more direct approach to the hypothesis of a relationship between flexibility and invasiveness, by comparing the flexibility, both at the outcome and at the process levels, shown by an invasive species and the native species it displaces.

Our study model was a population of free-ranging invasive grey squirrels (*Sciurus carolinensis*) and a population of native red squirrels (*S. vulgaris*) in the UK, and we compared their flexibility, at the outcome level, by measuring their success in solving food-extraction problems in field experiments. Although grey squirrels are larger than red squirrels (Bryce, Speakman, Johnson, & Macdonald, 2001), the two species share many morphological and ecological characteristics, so that niche overlap is high, see Koprowski (1994) for grey squirrels and Lurz, Gurnell, & Magris (2005) for red squirrels. Grey squirrels are regarded as one of the '100 World's Worst Invasive Alien Species' (Lowe, Browne, & Boudjelas, 2008). They were introduced to the UK and Ireland in the 19th century (Gurnell, 1987) and more recently to Italy (Bertolino, Lurz, Sanderson, & Rushton, 2008; Martinoli, Bertolino, Preatoni, Balduzzi, Marsan et al., 2010), and in all three countries the population of grey squirrels is still expanding (Huxley, 2003; Bosch & Lurz, 2012) and replacing red squirrels. When red squirrels in European countries are sympatric and have to compete with grey squirrels, they spend less time foraging and consume less high-energy food than their counterparts that live without the grey squirrels (Wauters, Gurnell, & Martinoli, 2001; Wauters, Tosi, & Gurnell, 2002). Measurable consequences of the competitive interactions between the species include significantly reduced red squirrel reproductive success and

74 juvenile recruitment, leading to a potentially rapid decline of the local red squirrel population
75 (Gurnell, Wauters, Lurz, & Tosi, 2004). The red-grey squirrel system is therefore ideal for
76 investigating whether differences in behavioural flexibility may play a part in the competitive
77 success of the introduced species.
78
79 We first examined whether flexibility, at the outcome level, was different in the two
80 species, using the food-extraction problem paradigm (review by Griffin & Guez, 2014).
81 Based on invasion history in the UK (e.g. Gurnell, Lurz, & Bertoldi, 2014), we predicted that
82 grey squirrels would be more successful and efficient than the congeneric red squirrels in
83 solving problems. It has already been shown that grey squirrels show better spatial memory
84 than red squirrels (Macdonald, 1997), but this may be an example of niche-specific cognition
85 since red squirrels are less dependent on recovering scatter-hoarded caches than grey
86 squirrels (Bosch & Lurz, 2012).
87
88 We then investigated whether flexibility, considered as a process, was a trait that
89 predicts the differences in problem-solving performance at both between-species and within-
90 species levels. To examine this, we followed Chow et al. (2016), by measuring such
91 'flexibility' as the rate of switching between tactics after a failed attempt (hereafter
92 'instantaneous flexibility') to solve a given problem. Across species, problem-solving
93 performance is not always a function of instantaneous flexibility: Other traits such as
94 persistence (rate of attempts), motor diversity (rate of emitting new types of behaviour), and
95 selectivity (the proportion of effective behaviours emitted) have often been implicated. For
96 example, successful problem solvers showed increased persistence (Biondi, Bo, & Vassallo,
97 2008; Benson-Amram & Holekamp, 2012; Chow et al., 2016; Griffin et al., 2014; Van Horik
98 & Madden, 2016) and/or high motor diversity (Benson-Amram & Holekamp, 2012; Griffin et

al., 2014; Griffin & Diquelou, 2015; Diquelou et al., 2016). Enhanced efficiency as a result of practice can be related to increased persistence and increased selectivity (Chow et al., 2016), or decreased motor diversity with increased experience (Griffin et al., 2014). Accordingly, we included these three behavioural traits, alongside instantaneous flexibility, when examining between- and within-species differences in problem solving.

Ideally, we would have compared red and grey squirrels living in the same habitat, to avoid any confound between environmental and species differences. However, this is not possible because once grey squirrels enter red squirrel habitats, either the number of red squirrels declines (often rapidly due to the added risk of squirrelpox virus disease transmission; Rushton, Lurz, Gurnell, & Fuller, 2000; Sainsbury, Nettleton, Gilray, & Gurnell, 2000) or the greys are removed by humans in an effort to prevent that happening (for an overview of the current removal project in Scotland, control operations and the pox issue, see https://scottishsquirrels.org.uk/about/project-overview/). We therefore had to study separate populations of the two species. Within the range of habitats currently occupied by red and grey squirrels in the UK, we matched our study sites as closely as we could for climate, season, vegetation types, predation risk, the number of foraging squirrels, and the level of human activity. We also used study sites as widely spread as possible within each habitat, to maximise the genetic diversity within our sample and in order to avoid sampling the same individuals from each population.

METHODS

Ethical note

Our study was approved by the Ethical Review Group at the University of Exeter (no. 2012/533). Experiments were carried out in accordance with Association for the Study of

Animal Behaviour guidelines on animal welfare and UK law. Initially, we used trapping method to identify individuals. Between April and September, 12 traps were set at different locations in the University of Exeter campus from dawn to dusk. Traps were checked every 1.5-2 hours. When a squirrel was captured, we transferred it to a mesh cylinder-shaped tube (or a handling cone). We PIT tagged and marked each squirrel with a different pattern at different body parts, using commercial hair dye. Individuals were released once they had been sexed and weighed. No deaths occurred as a result of trapping. As the trapping process appeared to deter squirrels from participating in these experiments (only 4 out of 43 trapped squirrels interacted with the test apparatus), we used the individuals' unique characteristics for identification for the rest of the experiment (see below '*Animal Identification*'). The experiments did not involve invasive methods; squirrels voluntarily approached and left the apparatus. The apparatus was placed away from roads and in locations with low risk of predation to avoid exposing the squirrels to added risk from participating in the experiments.

Study habitats, study sites and study populations

We collected data from two free-ranging squirrel populations in habitats that contained either grey squirrels or red squirrels exclusively. The grey squirrel habitat consisted of woodlands neighbouring the University of Exeter campus, Devon, England (50.74°N, 3.54°W), or on the campus itself. Data were collected from eight sites within this habitat, between October 2013 and January 2014, and between December 2014 and February 2015. The red squirrel habitat consisted of woodlands around Brodick castle and country park (55.59°N, 5.15°W), Brodick, Isle of Arran, Scotland. Data were collected from seven sites within this habitat, from September to November 2014. All sites were public areas, were 500-800 m apart, had low predation risk, and had three to five squirrels that foraged regularly within them. Both

habitats had exotic trees such as Sessile oak (*Quercus petraea*), Scots Pine (*Pinus sylvestris*), beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*).

Animal identification

Squirrels were identified from video recordings, using frame-by-frame analysis in the software Adobe Premiere Pro CS6. Most squirrels were identified using their unique characteristics such as coat colour, tail shape, body size, ear shape, and paw colour, as well as identifiable marks on face and body. This procedure required intensive observer training, typically around two months for each species. Four grey squirrels had been marked with black hair dye in a previous trapping effort to facilitate identification.

Apparatus and equipment

We designed two problems that could both be solved within squirrels' behavioural repertoire, but which varied in their expected difficulty so that we could observe a range of problem-solving ability. Fig. 1a shows the apparatus for the easy task. It consisted of a hinged box (12 x 12 x 4.5 cm, Length x Width x Height). It had four plastic wells, one at each corner (4.5 x 3 x 1.5 cm), and each well was covered by a hinged transparent lid (3 x 3 cm). Fig. 1b shows the apparatus for the difficult task. It consisted of the puzzle box that had been used in a laboratory study (Chow et al., 2016). This task was expected to be more difficult than the hinged box task for the squirrels, as it required counter-intuitive methods to solve it. The apparatus consisted of a transparent Plexiglas box (25 x 25 x 19 cm), which had ten holes (2 x 0.9 cm, W x H) located on each side, and a pyramid-shaped base (25 x 25 x 3 cm). The ten holes on each side of the box were horizontally but not vertically aligned with holes on the opposite side. Levers were inserted across the box through holes roughly opposite to each other. The box was secured above the base by four wooden legs so that there was a gap

between the box and the base, allowing a squirrel to obtain nuts when it had solved the problem. The gap for grey squirrels was 4.5 cm and for red squirrels was 3.5 cm, as red squirrels have shorter body length than grey squirrels. During the main testing, ten plastic levers were inserted through holes across the box, protruding from the box by 2.5 cm at each end. Each lever (1.5 x 29.8 x 0.5 cm; Length x Width x Thickness) had a 3-sided Plexiglas nut container (back: 2 x 1.5 cm; side: 1.5 x 1.5 cm) at one end; this was positioned just inside the box. The back of the nut container was transparent and its sides were white, so the squirrels could view the nut from two opposite sides of the box. This design allowed a squirrel to cause a lever to drop, and thereby obtain a nut if there was one in the nut container. This could be achieved by pushing the lever end that was near to the nut (henceforth, 'near end'), or by pulling it from the opposite end (henceforth, 'far end'). These tactics are referred to below as "effective". However, the problem could not be solved by the more intuitively obvious tactics of pulling at the near end or pushing the far end; these tactics are referred to below as "ineffective".

Figure 1

Procedures

Before the experiment started, an experimenter (i.e. the first author) chose a location that was away from main roads and that was covered by bushes and trees. This aimed to minimise risks to the squirrels from predation risk or vehicles. Once a suitable location was chosen, the experimenter placed hazelnuts in the shell and hazelnut kernels to attract squirrels. Baits were checked twice a day for three consecutive days before the experiment. We re-baited the sites twice a day if squirrels took the hazelnuts. In the main experiment, we set the easy task on the ground at a random position to minimise the chance of squirrels using box position as a cue to open a lid. However, squirrels could use the length and the width of the lid to indicate which side to lift. During testing, each well contained one hazel nut. Because the difficult

task was much larger than the hinged box, and object size has been shown to affect neophobic response (Mettke-Hoffmann, Rowe, Hayden, & Canoine, 2006) and in turn, problem-solving performance (Overington et al., 2011), we minimised any such effect for the difficult task by giving a 4-hour habituation period to squirrels (Overington et al., 2011; Webster & Lefebvre, 2001). During this period, we presented the transparent box without levers, and placed 10 shelled hazelnuts on each side of the box. All squirrels approached and explored the apparatus. While we did not observe neophobic responses to either task during the main experiment (see videos in the supplementary materials), we could not completely exclude the possibility that squirrels were still neophobic to the apparatuses when they were solving the task. The box was placed either 80 cm away from a tree or inside bushes and close to trees to minimise predation risks. The puzzle box had ten levers inserted during the main testing; five levers were baited with hazelnuts and five levers were empty (control). Squirrels were free to come and go from the box and thus the number of nuts that each individual obtained could vary between trials. To prevent squirrels from using the positions of the holes or the direction of the cover relative to the tree to solve the task, we randomised the side from which the levers were inserted, the direction of the nut containers, and which levers were baited with nuts between trials. The order of presentation of the two tasks was counter-balanced across sites.

Throughout the experiment, there were 2-4 squirrels active at each location. We took into account the individuals' varied active periods to minimise conspecific competition. We set up the apparatuses daily from dawn to dusk regardless of weather condition. We further re-baited the apparatus at one- to two-hour intervals. Accordingly, five to eight trials were carried out daily depending on the available daylight. This schedule allowed us to collect data from single individuals most of the time; fewer than 1% of attempts had two or more

individuals on or around the apparatus. In these situations, dominant squirrels chased subdominant squirrels away or subdominant squirrels would wait until the dominant squirrels left before approaching the apparatus. A video camera (Panasonic SWD HD-90) mounted on a tripod was placed 60 cm away from the apparatus to capture all task behaviours. During the data collection period with the grey squirrels, an experimenter (the first author) was present 25 m away from the apparatus in three of the eight locations, since these squirrels were relatively habituated to humans using the university campus.

Measurements

To compare between-species problem-solving performance, we first divided squirrels in each species into 'problem solvers' and 'non-solvers'. Problem solvers were squirrels that successfully solved the tasks repeatedly whereas non-solvers were those that never solved the tasks throughout the entire experiment, or that solved the tasks once but did not repeat that success on subsequent visits (squirrels that solved the problem more than once always went on to solve it multiple times). We then further divided problem solvers into 'first-time solvers' (those that solved the problems on their first visit) and 'subsequent solvers' (those that failed on their first visit but succeeded on a subsequent visit). A visit was recorded as starting when a squirrel was seen in the video to manipulate a lever or lid, and continued until it left the view of the video for two or more minutes. Visit durations largely reflected solving duration, but also included brief periods of visual 'inspection' of the apparatus. Success for the easy task was defined as a squirrel using its mouth, nose or front paw to lift up one of the four transparent lids. Success in the difficult task was defined as a squirrel using any of its body parts to manipulate a lever and causing the lever and/or a nut to drop.

To obtain detailed behavioural data about squirrels' problem-solving process, we focused on the behaviours that were exhibited during each attempt at problem solution. An attempt started when a squirrel used any of its body parts to contact a transparent lid in the easy task or a lever in the difficult task and ended when the squirrel stopped contacting that part of the apparatus. A new attempt was counted if the squirrel changed to manipulating another part of the apparatus. Attempts were counted regardless of whether the squirrel employed effective or ineffective behaviours for the task, and regardless of any switches between tactics exhibited and of the number of types of behaviour used. Recording attempts provided two measurements for each task:

Solving duration. We calculated each attempt duration as the time from when a squirrel used any of its body part to touch a lid/a lever to when the squirrel stopped touching the lid or lever (in the case of unsuccessful attempts) or when the squirrels opened a lid/made a lever and/or nut drop (in the case of success). The solving duration consisted of the sum of all attempt durations until a success occurred. Solving duration was our main measure of the efficiency of problem solving (i.e. how quickly a squirrel solved a task), but it was also used in our quantification of behavioural traits, as follows.

Persistence. Following previous authors (Biondi et al., 2008; Chow et al., 2016; Griffin et al., 2014), for each success, we obtained the total number of attempts, divided this number by the solving duration to obtain the rate of attempting to solve the problem, and used this as a measure of the behavioural trait persistence. Converting persistence to a rate allowed us to measure it independently of the inherent relationship between the number of attempts and solving duration (Chow et al., 2016). We regarded persistence as a measure of motivation for

problem solving (Griffin et al., 2014; Chow et al., 2016, Chow, Lea, Hempel de Ibarra, & Robert, 2017).

The difficult task allowed squirrels to exhibit different types of contact with the apparatus. This enabled us to measure three further behavioural traits, namely motor diversity, selectivity and instantaneous flexibility. Like persistence, motor diversity and instantaneous flexibility were measured as rates (frequency of occurrence/total solving duration to success) to minimise confounding with solving duration.

Motor diversity was measured as the rate of exhibiting different types of contact with the puzzle box, using the list of types shown in Table A1 (reproduced from Table 1 of Chow et al., 2016). Nine types of contact were recorded, including push up, push in, pull, tilt up, claw, lick, shake and two or more of these types of behaviours occurring simultaneously (hereafter, combined behaviours). Squirrels therefore received a score ranged from 1 to 9 as diversity. We then divided this number by their solving duration to obtain the rate of motor diversity.

Instantaneous flexibility was measured as the rate of switching between tactics. Using the definitions of contact types in Table A1, a switch was recorded whenever a squirrel changed from one type of tactic to another type after a failed attempt. Switches were recorded regardless of whether the current tactic has been previously used and regardless of whether the tactic was effective or ineffective. We obtained the total number of switches across attempts and divided this number by the total solving duration to obtain the rate of instantaneous flexibility.

294 *Selectivity* was measured as the proportion of effective behaviours shown. As noted above,
295 the effective behaviours were either pushing the 'near-end' or pulling the 'far-end' of a lever,
296 and ineffective behaviours were either pushing the 'far-end' or pulling the 'near-end'. We
297 obtained the number of effective behaviours that a squirrel exhibited and divided this number
298 by the total number of effective and ineffective behaviours to give our measure of selectivity.
299
300 *Statistical analyses*
301 For each task, we used Chi-square tests to compare the frequencies of individuals in the two
302 species that obtained success in their first visit and success in the subsequent visits.
303 Generalized Linear Model (GLM) was used to compare tasks' ('easy' or 'difficult') solving
304 duration on the first success for each species and to examine between-species ('grey' or 'red'
305 squirrels) differences in behavioural traits on the first success for the difficult task. To
306 examine how performance varied with experience, we chose a fixed number of successes,
307 after which little or no improvement in performance could be detected, and eliminated data
308 from squirrels that obtained fewer successes. For the easy task, we used data from the first
309 15 successes, and were able to include data from most of the squirrels (24 individuals, 11
310 grey and 13 red squirrels, 75% of the total). For the difficult task, performance took longer to
311 reach asymptote, and we used data from the first 40 successes, contributed by 18 individuals
312 (11 grey and 7 red squirrels, 42% of the sample). In the analysis for the easy task, we used the
313 Gamma log link function to accommodate values that were positively skewed but not
314 massively concentrated on or close to zero for continuous variables, and the Poisson log link
315 function for count variables. In the analysis for the difficult task, we used Generalized
316 Estimating Equations (GEE) with exchangeable working correlation (Liang & Zeger, 1986)
317 and Tweedie identity link function to accommodate mass values that were close to zero for
318 continuous variables. We included species, success number and their interaction as

independent variables when analysing solution time across success number. GEE was also used to examine between- and within- species differences in each behavioural trait. Finally, GEE was used to examine what factors were associated with enhanced efficiency in the difficult task for each species. For this analysis, we log-transformed the solution times to normalise their distribution before applying the Gaussian distribution for model estimation. Pearson correlations were used to investigate highly correlated variables (i.e. $r > 0.5$; see supplementary material Table A2). As motor diversity and persistence were highly correlated in both species ($r = 0.74$ for red squirrels and $r = 0.89$ for grey squirrels), we minimised confusion in interpreting the results by dropping motor diversity from the analyses. The decision to retain persistence over motor diversity was because persistence has been shown to be a key trait for this difficult task (Chow et al., 2016). Significance levels reported here are two-tailed and criterial level was $P \leq 0.05$. We further applied Bonferroni corrections to adjust the P values for multiple comparisons at between- and within- species levels, and significance level was then set at $P \leq 0.025$. All data were analysed using SPSS version 23.

RESULTS

Within-species task comparison

Task was a significant factor for solution duration in grey (GLM $\chi^2_1 = 7.81$, $P = 0.005$) and red squirrels ($\chi^2_1 = 9.68$, $P = 0.002$); the solution duration in the difficult task on the first success was significantly higher than in the easy task for both species. On their first success, grey squirrels took a mean of 4.3s (SE ± 1.2s) to solve the easy task whereas they took 12.7s (SE ± 4.7s) to solve the difficult task. Red squirrels took a mean of 3.9s (SE ± 0.7s) to solve the easy task on their first success whereas they took 9.4s (SE ± 2.1s) to solve the difficult task. This confirmed that, as intended, the puzzle box was more difficult than the hinged box for the squirrels.

Performance in the easy task

14 grey squirrels and 18 red squirrels attempted the easy task. Of these squirrels, 13 (93%) grey and 9 (50%) red squirrels solved the task on their first visit. This species difference in first-time success in solving the easy task was significant (Fisher's exact test: $P = 0.019$). Amongst these first-time solvers, grey squirrels spent an average of 4.2s (SE ± 1.3s) solving the task whereas red squirrels spent an average of 1.6s (SE ± 0.2s) to solve the task. This species difference in first-time solvers' solving duration was significant (GLM $\chi^2_1 = 9.27$, $P = 0.002$). Red squirrel non-solvers spent significantly longer time manipulating the task on their first visit (Mean = 5.19s, SE ± 8.8s) than red squirrel problem solvers ($\chi^2_1 = 5.66$, $P = 0.017$), but their manipulation times did not differ significantly from those of grey squirrel problem solvers ($\chi^2_1 = 0.72$, $P = 0.396$).

The squirrels that did not succeed on their first visit all succeeded on subsequent visits (see *Within-species task comparison* above for the mean and standard errors of the solving duration on the first success in the easy task for each species, for the 14 grey and 18 red squirrel problem solvers). Fig. 2a shows the solving duration for the 24 squirrels (11 grey and 13 red) that completed 15 successes. Species did not differ in solving duration (GEE $\chi^2_1 = 1.40$, $P = 0.237$). All squirrels increased their efficiency with experience of success ($\chi^2_1 = 18.59$, $P < 0.001$). The interaction between species and success number was not significant ($\chi^2_1 = 0.98$, $P = 0.323$).

Fig. 2b shows how attempt rate, our measure of persistence, varied with experience and species. It was significantly higher in the grey squirrels than the red squirrels ($\chi^2_1 = 4.95$, $P = 0.026$). Attempt rate increased with increased success number ($\chi^2_1 = 79.44$, $P < 0.001$). Its

interaction with species was also significant ($\chi^2_1 = 10.51$, $P = 0.001$); as Fig. 2b shows, with increased experience of success, attempt rate decreased in grey squirrels but increased in red squirrels. These results may reflect the two species using different strategies to interact with the task (e.g. grey squirrels may make few long-bout attempts whereas red squirrels may make more short-bout attempts across the success number). To understand this further, we focused on whether the two species differed in their actual number of attempts made and the mean duration of each attempt (i.e. solving duration/the number of attempts) when solving the easy task. Figure 2c shows the actual number of attempts made across 15 successes. Success number had a significant main effect ($\chi^2_1 = 21.27$, $P < 0.001$); the number of attempts decreased across the 15 successes. Neither species ($\chi^2_1 = 0.88$, $P = 0.348$) nor the interaction between species and success number were significant ($\chi^2_1 = 0.35$, $P = 0.851$). Figure 2d shows the length of each attempt across 15 successes for each species. Species differed significantly in the mean attempt duration across 15 successes ($\chi^2_1 = 4.40$, $P = 0.036$); grey squirrels made shorter attempts than red squirrels. Both species decreased the duration of each attempt across 15 successes ($\chi^2_1 = 19.04$, $P < 0.001$) and the interaction of species with success number was also significant ($\chi^2_1 = 4.64$, $P = 0.031$); across successes, red squirrels decreased the mean duration of an attempt bout more quickly than grey squirrels.

Figure 2

Performance in the difficult task

All squirrels that participated in the easy task also participated in the difficult task. A further eight grey and three red squirrels participated in the difficult task, which yielded a total sample size of 43 (22 grey and 21 red squirrels) for this task. Fig. 3a left panel shows that 14/22 (64%) grey and 6/21 (29%) red squirrels succeeded on their first visit (first-time solvers). The species differed significantly in the frequency of problem-solving success on their first visit (Fisher's exact test: $P = 0.021$). These first-time solvers' solving duration did

not differ significantly between species (GLM: $\chi^2_1 = 1.58$, $P = 0.209$), although grey squirrels tended to take longer (Mean = 12.3s, SE ± 6.8s) than red squirrels (Mean = 5.7s, SE ± 2.4s) to solve the task on their first visit. Red squirrel non-solvers' time spent on manipulating the task on their first visit did not differ significantly from that of their conspecifics who were first-time solvers ($\chi^2_1 = 3.07$, $P = 0.080$), but they spent significantly less time than grey squirrel problem solvers ($\chi^2_1 = 14.32$, $P < 0.001$) on the first visit.

Fig. 3a right panel shows that 20/22 (91%) grey squirrels and 13/21 (62%) red squirrels solved the task on either their first or a subsequent visit; the difference between these frequencies was also significant (Fisher's exact test: $P = 0.039$). Fig. 3b shows the mean solving duration for the 11 grey and 7 red squirrels that completed 40 successes. Among these successful problem solvers, species differed significantly in solving duration across 40 successes (GEE $\chi^2_1 = 5.13$, $P = 0.024$); the red squirrels were faster than the grey squirrels, in solving the difficult task (see *Within-species task comparison* above for the mean and standard errors of solving duration in the difficult task). Squirrels increased efficiency with increased experience ($\chi^2_1 = 8.34$, $P = 0.004$). The interaction between species and success number had no significant effect on efficiency ($\chi^2_1 = 0.81$, $P = 0.369$).

Figure 3

Difficult task: between-species' behavioural trait differences, solving success

On the first success, squirrels showed no significant species differences in any of the behavioural traits that we measured: rate of attempts (GLM $\chi^2_1 = 0.45$, $P = 0.504$, 20 grey and 13 red squirrel problem solvers), switch rate ($\chi^2_1 = 1.21$, $P = 0.272$), proportion of effective behaviours ($\chi^2_1 = 0.58$, $P = 0.447$) or rate of motor diversity ($\chi^2_1 = 0.01$, $P = 0.930$). For those squirrels that achieved 40 successes (11 grey and 7 red squirrel problem solvers), the two species differed significantly in the switch rate across these successes, our measure of

instantaneous flexibility (GEE: $\chi^2_1 = 7.03$, $P = 0.008$, $P < 0.025$ after Bonferroni correction), but not in rate of attempts ($\chi^2_1 = 0.62$, $P = 0.432$), rate of motor diversity ($\chi^2_1 = 3.53$, $P = 0.060$), or the proportion of effective behaviours ($\chi^2_1 = 0.44$, $P = 0.506$). Grey squirrel problem solvers showed lower switch rates than the red squirrel problem solvers.

Difficult task: within-species' behavioural traits and solving duration

Table 1 shows the varied contribution of behavioural traits to solving duration for each species. Grey squirrels increased efficiency was associated with a higher rate of attempts ($P < 0.001$) and proportion of effective behaviours ($P < 0.001$) whereas red squirrels enhanced efficiency was related to a higher rate of attempts ($P < 0.001$), proportion of effective behaviours ($P < 0.001$) and level of instantaneous flexibility ($P < 0.001$).

Table 1

Difficult task: within-species' behavioural traits and solving success

Because almost all grey squirrels successfully solved the difficult task, within-species' differences in traits and performance between solvers and non-solvers could only be analysed in red squirrels. To examine the differences between problem solvers and non-solvers, we investigated the minimal attempts that most non-solvers made. Seven out of eight non-solvers made at least 15 attempts. Accordingly, these non-solvers, along with all subsequent solvers (N=7) and first-time solvers (N=6) were included in this within-species analyses.

Solving duration was not significantly different between non-solvers and first-time solvers ($\chi^2_2 = 1.70$, $P = 0.192$, Fig. 4a) or between non-solvers and subsequent solvers ($\chi^2_2 = 2.04$, $P = 0.154$, Fig. 4a). Fig. 4b and c show the proportion of effective behaviours and the rate of motor diversity for the three types of solvers. Neither trait showed a significant difference between first-time solvers and non-solvers (selectivity: $\chi^2_2 = 1.97$; $P = 0.161$; rate of motor

diversity: $\chi^2_2 = 4.37$; $P = 0.037$, *NS* after Bonferroni correction) or between subsequent solvers and non-solvers (selectivity: $\chi^2_2 = 4.73$; $P = 0.030$, *NS* after Bonferroni correction; rate of motor diversity: $\chi^2_2 = 0.039$; $P = 0.844$). Fig. 4d shows the rate of instantaneous flexibility for the three types of solvers. Non-solvers showed significantly lower switch rates than first-time solvers ($\chi^2_1 = 13.68$; $P < 0.001$; $P < 0.025$ after Bonferroni correction), but their rates were not different from those of subsequent solvers ($\chi^2_1 = 0.71$; $P = 0.401$). We also examined the rate of producing productive switches (i.e. when squirrels switch from ineffective to effective behaviours after a failed attempt). Fig. 4e shows the rate of productive switches among the three categories of squirrel. Non-solvers showed a significantly lower rate of productive switches than first-time solvers ($\chi^2_2 = 13.68$; $P < 0.001$, $P < 0.025$ after Bonferroni correction) and subsequent solvers ($\chi^2_2 = 13.68$; $P < 0.001$, $P < 0.025$ after Bonferroni correction).

Figure 4

DISCUSSION

Using two food-extraction tasks, we provide the first detailed empirical study of the differences in the level of flexibility between an invasive and a native mammalian species that compete with each other. In between-species analyses, our results indicate that invasive grey squirrels have higher behavioural flexibility at the outcome level than native red squirrels. The grey squirrels were more likely than the reds to solve the easy task on their first visit, and a higher proportion of grey than red squirrels solved the difficult task. However, red squirrel problem solvers showed comparable solving duration to grey squirrel problem solvers in the easy task, and among the squirrels that did solve the difficult task, grey squirrels were less efficient than red squirrels. At within-species level, red squirrel problem solvers' increased efficiency was associated with an increase in instantaneous flexibility, and failure in problem solving was associated with low instantaneous flexibility. Together, these

data reveal that flexibility overlaps between the two species, but with a much wider range of problem-solving ability in the red squirrels than in the grey squirrels. Analyses of the contributions of problem-solving related behavioural traits showed that there are both similarities and differences between the two species in the problem-solving processes.

The high success rate of grey squirrels in solving the easy problem on the first visit (93%) and the difficult problem (91%) show that this invasive species has an advantage in problem solving. Grey squirrels have replaced the native red squirrels in most habitats in the UK and Ireland, and parts of northern Italy. This successful invasion might reflect inherently high (or 'superior' as it is termed in other references e.g. Elton, 1958; Sakai, Allendorf, Holt, Lodge, Molofsky et al., 2001) flexibility in grey squirrels. However, the higher problem-solving ability we observed could also be explained by selective pressure during the invasion process, if enhanced flexibility is favoured as a trait when invading a new environment (Wright, Eberhard, Hobson, Avery, & Russello, 2010). To disentangle inherent capacity from selective pressure, it would be necessary to compare the grey squirrels' problem-solving ability in a non-native environment with their problem-solving ability in their native environment in Eastern North America.

Given an easy problem, red squirrels non-solvers spent longer manipulating the task than their counterpart solvers and comparable amount of time to grey squirrels problem solvers, but still failed to solve the problem on their first visit. Given a more difficult problem, the majority of red squirrels (71%) failed to solve it on their first visit (Fig. 3a). Even though the 29% of the red squirrels that did solve the difficult task at their first visit showed comparable solving efficiency to grey squirrels, and those red squirrels that completed 40 successes came to outperform the grey squirrels with increased successes (Fig.

3b), these results indicate that at the population level the native red squirrels are less flexible at the outcome level than grey squirrels. Our analysis at within-species level further indicates that instantaneous flexibility, flexibility at the process level, was low among the red squirrel non-solvers. Where the two species co-exist, red squirrels' foraging efficiency is depressed (Wauters et al., 2001, 2002), but since the habitats we used only had a single species, our results could not be due to such a competitive effect. Yet, clear differences in problem-solving ability were observed. Although the habitats in which we observed the two species were not completely identical, as far as we know, none of the differences between them has been shown to correlate with differences in problem-solving performance. Accordingly, a difference in behavioural flexibility may be added to the causes that lead to the red squirrels' population decline, alongside competition for food sources (Wauters et al., 2001, 2002) and squirrelpox (Rushton, Lurz, Gurnell, & Nettleton, 2006). Problem-solving ability will be critical for both species in resource exploitation and survival, so differences in flexibility may contribute to the observed patterns of species replacement, an aspect of the situation that has been completely unexplored up to now.

The facts that all squirrels eventually solved the easy task, and that some red squirrels solved the difficult task and did so efficiently, show that problem-solving ability overlaps between the two species. Our analyses showed that the two species have both similarities and differences in problem solving. For the easy task, both red and grey squirrels showed comparable solving duration, but the two species were using different strategies to achieve efficiency; grey squirrels decreased attempt rate whereas red squirrels increased attempt rate across successes (Fig. 2b). The difference was due to grey squirrels making more, shorter attempt bouts whereas red squirrels made fewer, longer attempt bouts (Fig. 2d). For the difficult task, red and grey squirrels are similar in that in both species enhanced efficiency

was associated with increased persistence (the attempt rate) and selectivity (the proportion of effective behaviours). These two traits have been found to be associated with efficiency in our previous studies with captive grey squirrels solving this difficult task (Chow et al., 2016), and are similar to findings in other species, for example Indian mynas, pheasants, hyenas, and meerkats (Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012; Griffin et al., 2014; Van Horik & Madden, 2016). The differences in the species' problem-solving processes lay in the effects of instantaneous flexibility. In red squirrels, but not grey squirrels, instantaneous flexibility increased efficiency among those animals that solved the problem repeatedly (Table 1). Our measure of instantaneous flexibility has been shown to be related to memory in this puzzle box (Chow et al., 2017), and ability to produce a switch from ineffective to effective tactic requires the individuals to remember the effective tactic. Given that the relationship between instantaneous flexibility and selectivity was positive for the small proportion of red squirrels that were problem solvers, but negative for the grey squirrel problem solvers (Table A2), it seems that these red squirrels, at least, have better memory for their past actions than the grey squirrel problem solvers. It follows that individual variation in problem-solving ability may be wider in red squirrels than grey squirrels.

The fact that non-solvers' failure lies in flexibility-related traits raises several questions, including whether low flexibility is correlated with other sub-optimal behavioural adjustments such as decreased foraging time and consuming low energy food, which have been observed when red squirrels cohabit with grey squirrels (Wauters et al., 2001, Wauters et al., 2002); and whether low flexibility is associated with measureable negative consequences in fitness. Although these questions remain to be investigated, inefficient foraging behaviours, including inefficient food-extraction, are predicted to decrease fitness, they necessarily reduce the chances that red squirrel juveniles would be equipped for

reproduction. Reduced reproductive success is a major factor for the decline of red squirrels (Gurnell et al., 2004), alongside squirrelpox (Rushton et al., 2006) and food competition (Wauters et al., 2001, Wauters et al., 2002).

Conclusion

Using two food-extraction tasks, we provide evidence for differences in behavioural flexibility between an invasive mammalian and a related native species. Our results show that invasive grey squirrels are more successful than the native red squirrels in solving a difficult problem, but the few red squirrels that solved the problem outperformed their grey congeners in efficiency. These results suggest that flexibility overlaps between the two species, but with a wider range of problem-solving ability in the red squirrels than in the grey squirrels. Overall, our results suggest that differences in behavioural flexibility, leading to more successful problem solving, could play a part in explaining the replacement of native red squirrels by the grey invaders.

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Appendix

Table A1. The type of behavioural tactics that squirrels used to solve the puzzle box task.

Information is Table 1 extracted from (Chow, Lea and Leaver, 2016).

Behaviours		Definitions
Pull	Effective*	A squirrel uses its teeth to make an outward movement and a lever subsequently moves outside the box. This pulling behaviour must be performed on the near end of the nut container.
	Ineffective#	A squirrel uses its teeth to make an outward movement and a lever does not move out of the box. This pulling behaviour must be performed on the *far* end of the nut container.
Push	Effective*	A squirrel uses any of its body part, including nose (usually), teeth, paw or chin to make an inward movement of a lever and the lever subsequently moves inside the box. This pushing behaviour must be performed on the *near* end of the nut container.
	Ineffective#	A squirrel uses any of its body part, including nose (usually), mouth, teeth, paw or chin to make an inward movement of a lever and the lever would not move. This pushing behaviour must be performed on the far end of the nut container.
Push up		A squirrel uses its nose to make a push under an end of a lever.
Push down		A squirrel puts force on a lever end with its paws or teeth. This behaviour makes the lever appear in a curved shape.
Tilted up		A squirrel uses its nose to level up a lever end. This behaviour makes a lever turn 45 degrees.
Claw		A squirrel uses it front paws to scratch a lever end.
Lick		A squirrel uses its tongue to touch a lever end.
Shake		A squirrel uses its teeth to bite a lever end causing an up-and-down movement.
Combined behaviours		At least two of the behavioural types that mentioned above appear.

* indicated as direct effective contact types.
# indicated as non-effective contact types.

Table A2. Pearson correlations between traits within each species. Correlations at the top part are for grey squirrel problem solvers (*N*=11) whereas correlations at the lower part are for red squirrel problem solvers (*N*=7).

	Success number	Persistence	Selectivity	Instantaneous flexibility	Motor diversity
Success number	-	-0.01	0.17	0.07	0.01
Persistence	0.10	-	0.36	0.27	0.89
Selectivity	0.43	0.28	-	-0.06	0.34
Instantaneous flexibility	0.12	-0.07	0.09	-	0.62
Motor diversity	0.14	0.74	0.24	0.04	-

561 **Figure captions**

562 **Figure 1.** a) an easy task: a hinged box that is constructed with four containers, one at each
563 corner. Squirrels could lift up a lid using their front paw, nose or teeth to obtain a hazelnut. b)
564 a difficult task: the puzzle box that has been used in Chow et al. (2016). It is a transparent
565 box, constructed with 10 holes that are randomly located on each side. Squirrels could solve
566 the task by pushing the near-end (close to the reward) or pulling the far-end (far from the
567 reward).

568 **Figure 2.** Easy task: across 15 successes, 24 squirrels' (N_{grey} = 11, N_{red} = 13) a) mean solving
569 duration; b) mean attempt rate; c) mean number of attempts; and d) mean length per attempt
570 (i.e. attempt duration) in seconds.

571 **Figure 3.** Difficult task: percentage of problem solvers obtained first success in each species
572 (N_{grey} = 22, N_{red} = 21) on their first visit (left panel) and either on the first or at a subsequent
573 visit (right panel). The number above each bar indicates the actual number of squirrels that
574 successfully solved the task. *P<0.05. b) mean solving duration in seconds for 18 individuals
575 that had completed 40 successes (N_{grey} = 11, N_{red} = 7).

576 **Figure 4**. Within-species analysis: box plot of each behavioural trait for non-solvers (N = 7),
577 subsequent solvers (N = 7) and first-time solvers (N = 6). Whiskers of a box indicate
578 minimum and maximum values, edges of the box indicate first and third quartiles and the
579 internal line of the box indicates median. a) solving duration; b) selectivity, the proportion of
580 effective behaviour; c) motor diversity, the rate of exhibiting different types of behaviours; d)
581 instantaneous flexibility, the rate of switching between tactics after a failed attempt,
582 regardless whether the tactic has been previously used; e) productive switch, the rate of
583 switching from ineffective to effective tactics. *<0.05, **<0.01, ***<0.001

Figure 1

Figure 2

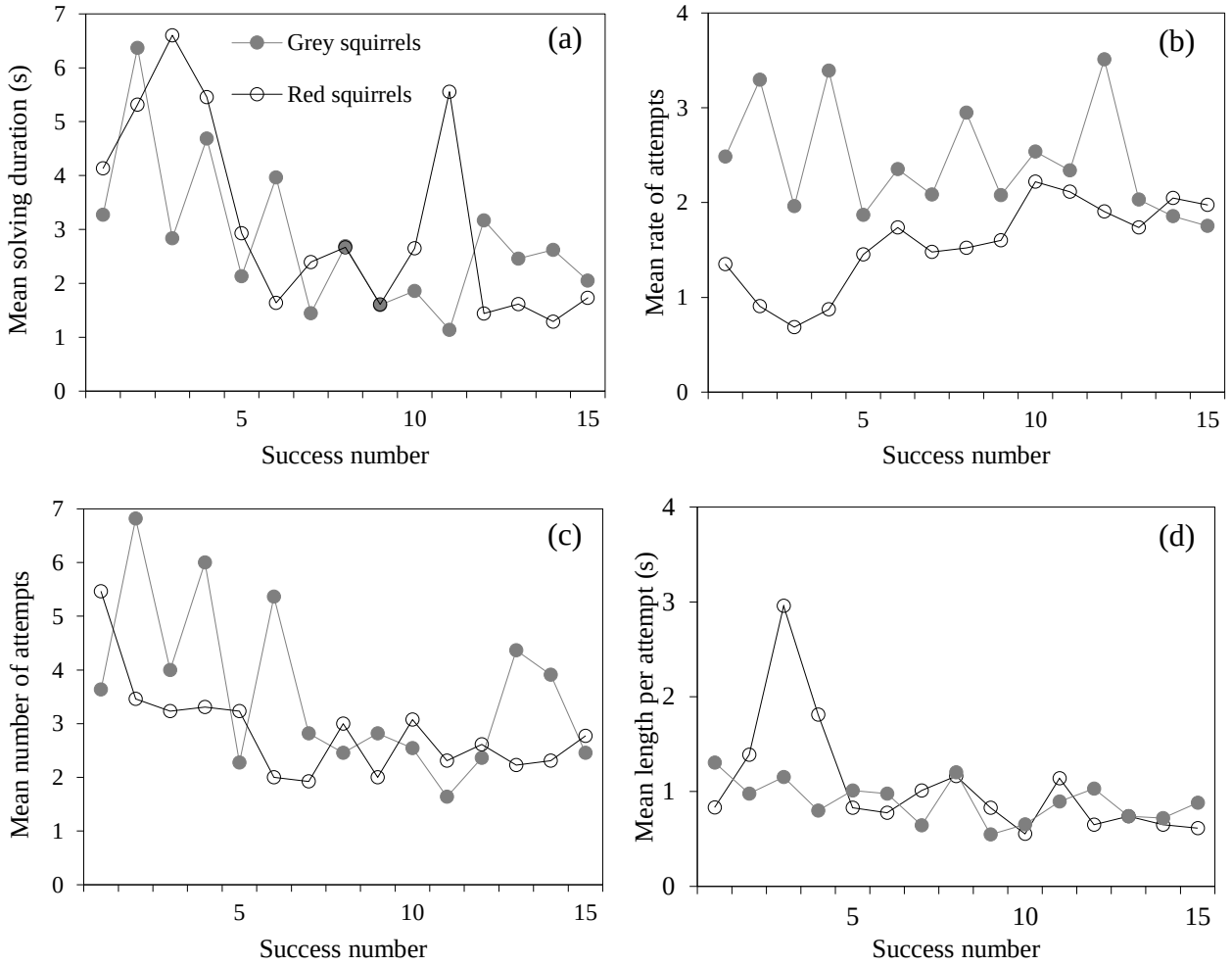
(a)
Grey squirrels
Red squirrels
Mean solving duration (s)
Success number
(b)
Mean rate of attempts
Success number
(c)
Mean number of attempts
Success number
(d)
Mean length per attempt (s)
Success number

Figure 3

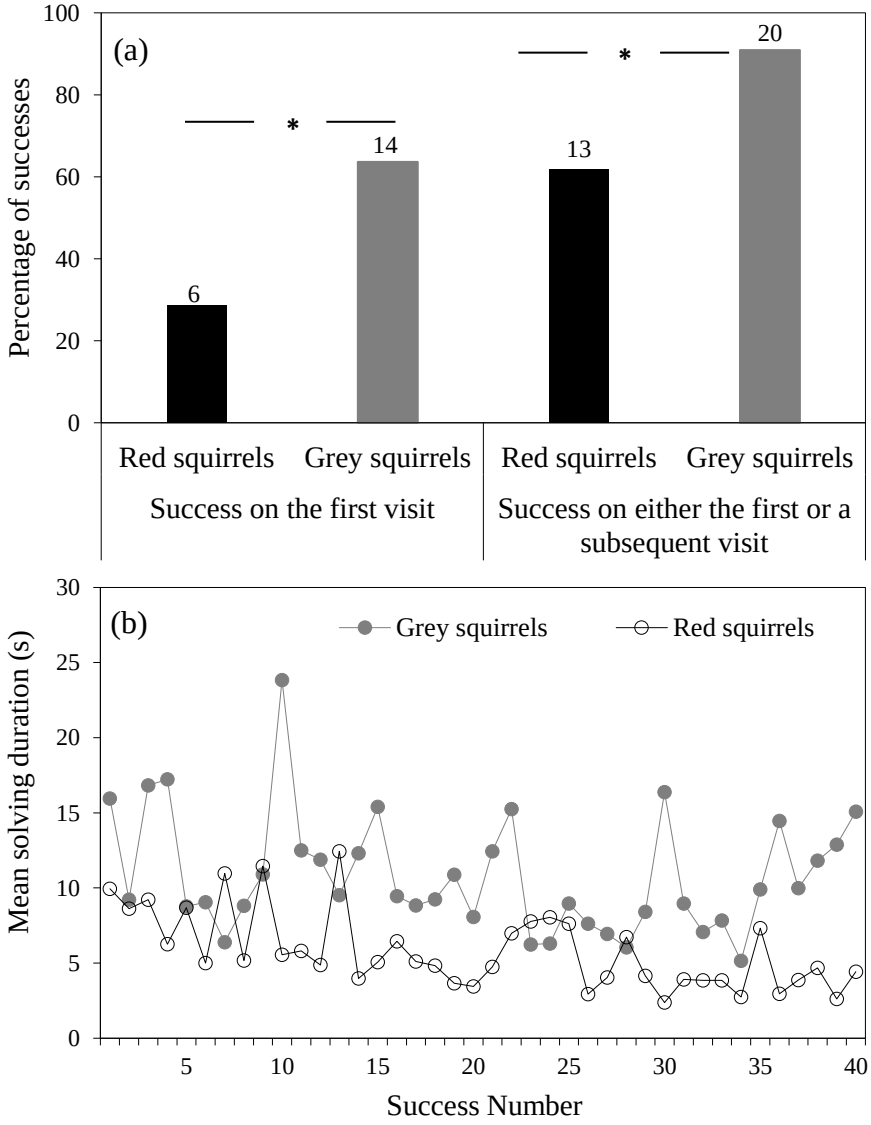
(a)
Percentage of successes
100
80
60
40
20
0
6
14
13
20
*
*
Red squirrels
Grey squirrels
Red squirrels
Grey squirrels
Success on the first visit
Success on either the first or a subsequent visit
(b)
Grey squirrels
Red squirrels
Mean solving duration (s)
30
25
20
15
10
5
0
5
10
15
20
25
30
35
40
Success Number

Figure 4

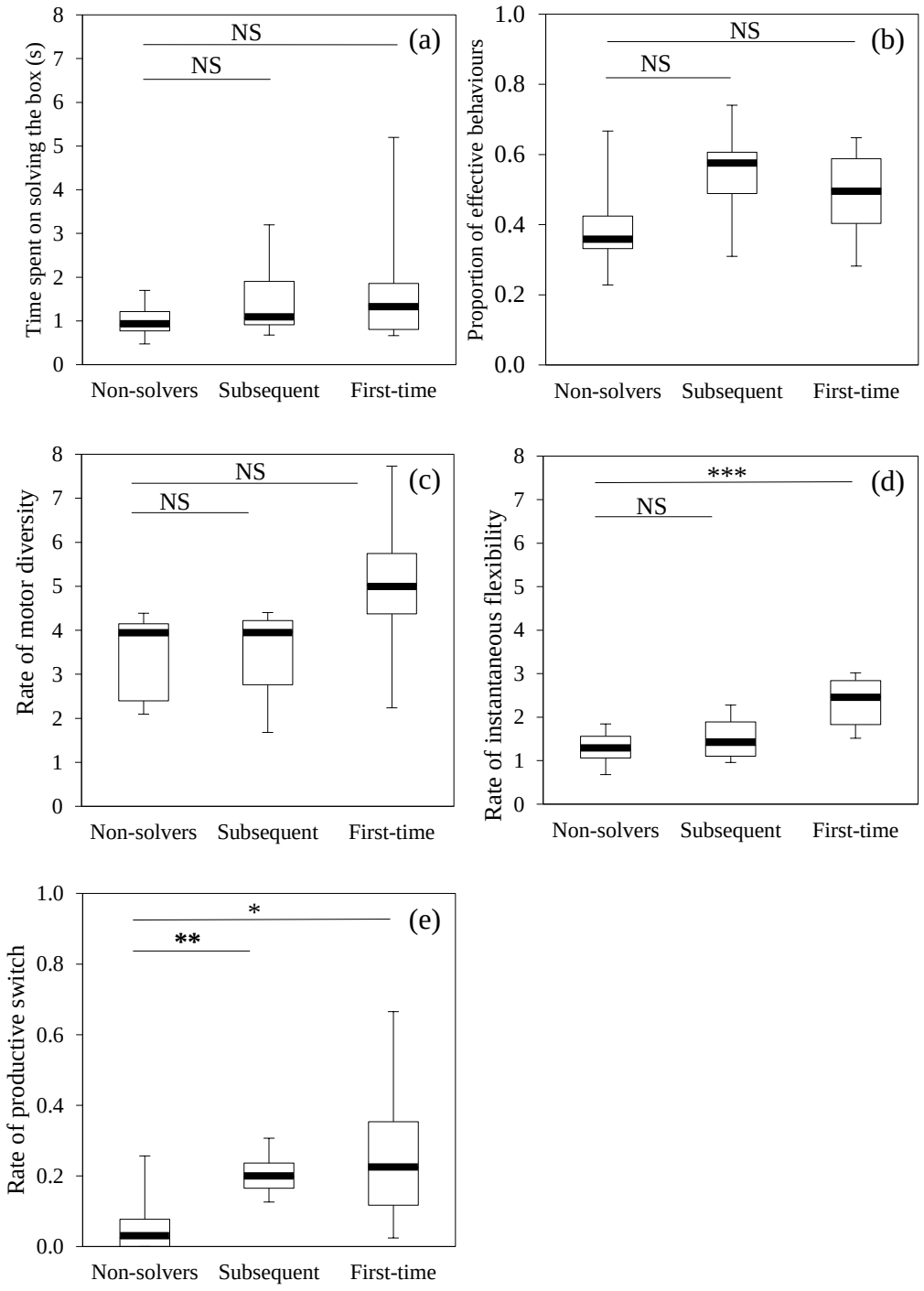
(a)
Time spent on solving the box (s)
NS
NS
(b)
Proportion of effective behaviours
NS
NS
(c)
Rate of motor diversity
NS
NS
(d)
Rate of instantaneous flexibility
***
NS
(e)
Rate of productive switch
*
**
Non-solvers
Subsequent
First-time

Table 1. Puzzle box task: GEE models examining the varied contribution of behavioural traits to problem-solving efficiency for each species (N_{grey} = 11, N_{red} = 7).

		40 successes				
Species	Independent variable	Estimates	SE	*df*	χ^2	P
Grey squirrels (*N*=11)	Success number	<0.01	<0.01	1	3.38	0.066
	Persistence	-0.10	0.01	1	95.78	**<0.001**
	Selectivity	-1.08	0.12	1	81.04	**<0.001**
	Instantaneous flexibility	-0.01	0.02	1	0.21	0.644
Red squirrels (*N*=7)	Success number	<-0.01	>0.01	1	1.60	0.206
	Persistence	-0.09	0.01	1	317.47	**<0.001**
	Selectivity	-0.37	0.11	1	11.09	**0.001**
	Instantaneous flexibility	-0.05	0.01	1	34.32	**<0.001**

Note: Factors include success number (40 trials), persistence (rate of attempts), selectivity (proportion of effective behaviours), and instantaneous flexibility (rate of switching between tactics). The table includes estimates, SE, df, χ^2 and P values.